EFFECTS OF INVESTIGATOR ACTIVITY ON RING-BILLED GULL BEHAVIOR AND REPRODUCTIVE PERFORMANCE

PETER M. FETTEROLF

Human disturbance can be a detriment to hatching success in Herring Gulls (*Larus argentatus*) (Hunt 1972) and Western Gulls (*L. occidentalis*) (Robert and Ralph 1975). The activities of scientists can also cause significant reductions in fledging success (Glaucous-winged Gull [*L. glaucescens*]) (Gillett et al. 1975). These studies and others (Emlen 1956, Tinbergen 1960, Ashmole 1963, Harris 1964, Kadlec et al. 1969, Anderson and Keith 1980) have reported the behavior of chicks in response to human intrusion but none has quantified the observed behavior of adults and chicks. In this study I: (1) quantify human disturbance effects on Ring-billed Gull (*L. delawarensis*) adult and chick behavior, as well as reproductive performance; (2) compare past findings on reproductive performance to data I collected at two different colonies in four different years; and (3) examine the theoretical ramifications of biased reproductive performance resulting from human activity.

STUDY AREAS AND METHODS

Mugg's Island.—I collected data on gull behavior and reproductive performance on Mugg's Island, Toronto Harbour, Toronto, York RM, Ontario, Canada, from April through July 1976–1978. The colony is inhabited by about 6000 pairs of Ring-billed Gulls and 50 pairs of Herring Gulls. The site is described elsewhere (Fetterolf 1979a).

Three study plots were located 2–7 m from an observation blind on top of a hill in the eastern section of the colony (Fig. 1). Each plot measured 7 × 14 m and half of each supported only very sparse vegetation (open habitat). The other half had little or no vegetation but was cluttered with driftwood and wooden stakes (1 × 3 × 40 cm) (driftwood habitat) which I placed in the areas in late fall of 1975. The open habitat sections of plots 1 and 3 had a few emergent sandbar willows (*Salix interior*) (0.10–0.75 m high) growing at one end of the section.

Eastern Headland.—I gathered data on reproductive performance at 17:30 on 27 June 1980 at the Eastern Headland, Toronto Outer Harbour (for description of the site see Blokpoel and Fetterolf 1978). The sampling area (15 × 30 m) was situated amongst about 4000 Ring-billed Gull nests and was nearly devoid of vegetation. Two clumps of lamb's-quarters (*Chenopodium album*) and two pieces of wood delimited the sampling area.

Disturbance regimes.—The level of investigator activity in each plot at each colony is summarized for each year in Table 1. I documented the effects of investigator activity on gull behavior only in 1977 on Mugg's Island.

Nest checks prior to hatching of eggs.—To determine the number of eggs laid in each nest on Mugg's Island, my assistant and I visited each plot every second day if there was no precipitation. We marked eggs with a felt-tipped pen, staked nests with numbered tongue
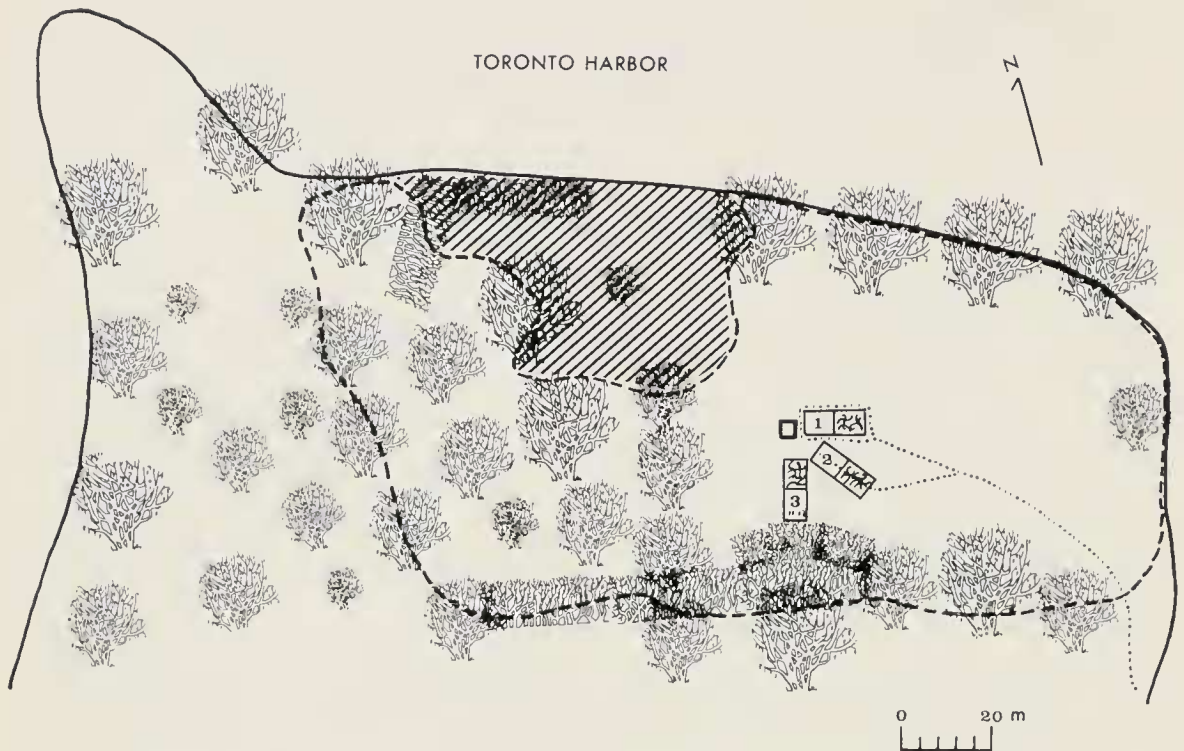
FIG. 1. Map of northeastern end of Mugg's Island showing the study plots, the nesting areas of Herring (////) and Ring-billed gulls (– – – –), and the route (· · · ·) taken by my assistant during experimental disturbances. Driftwood in each plot is represented by wavy lines.

depressors, and recorded time spent in each plot. On the Eastern Headland, the study area was entered only once during mid-incubation to count nests. Eggs and nests were not marked.

Observation of Investigator Activity After Onset of Hatch of Eggs, 1977

Documentation of gull behavior.—Every second day from 17 May until 3 June 1977, I documented the effects of investigator activity on gull behavior by observing from the blind while my assistant visited the moderately and most disturbed plots (plots 1 and 2, respectively; Fig. 1). I entered the observation blind at approximately 15:00 on the day prior to experimental disturbances by passing through the western edge of the moderately disturbed plot yet avoiding the other two plots. Each experimental session began at about 12:00 after I had spent the night in the blind to insure that disturbance during entry to the blind did not affect the results. For 30 min before my assistant entered the study plots, I continuously scanned all three plots to record behavior (pre-disturbance observation period).

At about 12:30 my assistant entered the colony from the southeast (Fig. 1) and checked nests in the moderately disturbed plot for hatching eggs while I recorded gull behavior (disturbance observation period). She walked

TABLE 1

INVESTIGATOR ACTIVITY IN EACH PLOT IN EACH YEAR ON MUGG'S ISLAND AND THE EASTERN HEADLAND

Plot	Year	Colony	Disturbance regime			
			Visits before hatching	Time in plot (min)	Visits after hatching	Time in plot (min)
1, 2, 3	1976	Mugg's Island	every 2nd day	15	every 2nd day	15
1 (Moderately disturbed)	1977	Mugg's Island	every 2nd day	7.8 ± 1.8[a,b] (N = 12)	every 2nd day	8.5 ± 4.5[c] (N = 9)
2 (Most disturbed)	1977	Mugg's Island	every 2nd day	5.8 ± 2.3[b,d] (N = 12)	every 2nd day	22.1 ± 11.2[c] (N = 9)
3 (Least disturbed)	1977	Mugg's Island	every 2nd day	9.3 ± 2.2[d] (N = 12)	once	5.9 (N = 1)
3[e]	1978	Mugg's Island	every 2nd day	6.5 ± 3.3 (N = 14)	not entered	—
—	1980	Eastern Headland	once	15	not entered	—

[a] Time in plots shown as means ± 1 SD, except where estimated.
[b] $t = 2.44$, df = 22. $P < 0.05$.
[c] $t = 3.40$, df = 16. $P < 0.01$.
[d] $t = 4.32$, df = 22. $P < 0.001$.
[e] Egg hatching in plots one and two was altered by exchanging eggs, so reproductive performance is not reported for these plots.

the perimeter of the plot, recorded the presence of newly emerged chicks and marked chicks without handling them using a weak picric acid solution sprayed from a plant mister. After checking each nest in the moderately disturbed plot, my assistant walked from the colony and I recorded behavior for 30 min in the plot (post-disturbance observation period). Following my 30 min post-disturbance watch, my assistant returned via the same route, entered the most disturbed plot and walked slowly to each nest while I recorded gull behavior (disturbance observation period). At the nest, she weighed freshly hatched chicks, banded them with expandable leg bands, and sprayed them with the picric acid solution. She then left the colony and I made a 30 min post-disturbance watch in the most and least disturbed plots. Visits were stopped when chicks in the moderately and most disturbed plots were at least a week old. The least disturbed plot was visited once after egg-pipping began (on 22 May) when my assistant and I checked hatching success in a few nests obscured by vegetation. No known human intrusions occurred in this plot after this date.

To document behavior I counted adult fights, chick runs, adult attacks on chicks, and the number of pecks delivered per attack. Behavior recorded as an adult fight included each or any combination of the following behaviors directed to another adult: (1) charging with wings outspread; (2) thrusting closed bill; and (3) grasping the bill or wing and tugging. I recorded a chick run whenever a chick walked or ran from its natal territory. Off the territory, I could not identify each individual chick because they often stopped and joined a group of young. Therefore, whenever a chick stopped running for at least 5 sec and then ran, I counted a chick run. An adult attack was recorded whenever an adult pecked or grasped and shook a chick. I counted the number of pecks in any attack and calculated the average pecks per attack (pecking rate). The reported values are probably low estimates because activity during (and often after) disturbance was so chaotic that events were likely missed.

Documentation of chick fates.—To measure the effects of investigator activity on the lives of chicks, I monitored the fate of chicks daily. Fates (decreases in brood-size which lasted at least 24 h after an experimental disturbance) were categorized as follows: (1) adopted by another pair; (2) pecked to death (observed or carcass with head laceration); (3) died on territory with no signs of pecking; and (4) unaccountably disappeared from the plot. Before each disturbance, I recorded the number of chicks at each nest in each plot. During and after the disturbance, I noted each death. Afterward, I identified the parentage of a dead chick, if unknown, using four indicators: (1) the location of the killing; (2) the estimated age of the chick and the number of chicks in similar-aged broods; (3) occasionally, the direction the chick was heading before death (chicks returning suc-

cessfully showed persistant directional running toward the natal territory); and (4) changes in the number of chicks attended by each pair of gulls. I also followed the fates of broods for 210 h during other behavioral observations lasting at least 4 h each day until early July when my watches became shorter.

Reproductive performance, 1977.—To establish the effects of human disturbance on reproduction, I recorded several measures of reproductive performance in each plot. Hatching success (number of eggs hatched/number of eggs laid) in the moderately and most disturbed plots was determined from the data collected during disturbances. I documented fledging success (number of chicks fledged/number of eggs hatched) for the moderately and most disturbed plots from the blind. Hatching and fledging success in the least disturbed plot were determined from the blind by noting the number of eggs and/or chicks for each pair. With two exceptions (two chicks of 26 days of age from a late nest), a chick was considered fledged at the age of 35 days when many Ring-billed Gulls are capable of flight. I counted all chicks which were hatched in the plot (color-marked with dye) and fledged from the plot as fledglings even though some individuals were adopted and reared by foster parents in the plot. I excluded from the analysis all undyed chicks from outside the plots that were adopted by pairs in the plot. I also excluded all chicks that hatched in the plot but were reared outside the plot by foster parents because I could not monitor their fates after adoption. Two chicks in the least disturbed plot were pecked to death by their parents after adoption of foreign chicks which were displaced from the adjacent, most disturbed plot during my assistant's visits. I therefore eliminated these deaths from the analysis of reproductive performance. I excluded the data from two late nests (probably renests) in the least disturbed plot because I could not determine the number of eggs or young in the nests which were partially obscured by vegetation. I use net reproductive output (number of chicks fledged/number of eggs laid) as a measure of overall reproductive performance.

To compare reproductive performance and behavior between plots, I divided the data into quarters based on the hatching date for the first egg hatched in each nest. I refer to first quarter gulls as 'early,' second and third quarter nesters as 'mid-season,' and fourth quarter birds as 'late.'

Reproductive Performance in Other Years

To determine whether reproductive performance depended more on the level of human disturbance during the post-hatching period, on the year data were gathered or on the colony in which it was obtained, I report reproductive performance from Mugg's Island in 1976 and 1978 as well as from the Eastern Headland in 1980.

Mugg's Island, 1976, 1978.—In 1976, nest checks continued every second day until eggs in all nests hatched or until 35 days after the nest had been initiated. Chicks were not

weighed, banded or marked with dye. In contrast with 1976, nest checks in 1978 were
discontinued after the first egg pipped and study plots were not approached during entry to
and departure from the blind. Hatching success was determined during visits in 1976 and
from the blind in 1978. I counted the number of fledglings at each nest from the blind in
both years.

Eastern Headland, 1980.—On Mugg's Island I observed that gull families remain in close
spatial proximity until chicks are at least 40 days of age. I considered a family to be one or
more chicks accompanied by at least one adult within one body length of the young. When
the oldest gull chicks were about 42 days of age on the Eastern Headland, I counted family
sizes from a 2-m step ladder concealed among 8–12 m cottonwoods (*Populus deltoides*) about
10 m from the sampling area. Most gulls were sitting in groups of one to three young with
one or two adults. I did not count groups of chicks unattended by an adult because chicks
from different broods sometimes huddle together when their parents are absent.

This sampling method does not account for nests that failed completely, i.e., produced no
fledglings, so the estimate of fledglings per nest must be scaled downward. Excluding the
most disturbed plot in 1977, the average rate of nest failure in six plots during 1976–1978 on
Mugg's Island was 7.8% (SD = 6.6). Assuming that there was a similar rate of nest failure
on the Headland in 1980, it is likely that 13 nests failed completely. Thirteen nests with zero
offspring were therefore added to the 172 families with at least one chick before I calculated
the number of fledglings per nest.

RESULTS

Observation of Investigator Activity, 1977

Nesting chronologies.—Different nesting chronologies in the least, mod-
erately, and most disturbed plots could affect interplot comparisons of
behavior and reproductive performance. Interplot comparisons of laying
and hatching chronologies revealed no significant differences (Kolgomo-
rov-Smirnov tests, $P > 0.05$). Egg-laying began on 19 April in all plots and
ended on 23 May in the moderately disturbed plot, on 30 May in the most
disturbed plot, and on 29 May in the least disturbed plot (excluding two
renests). The peak of egg-laying in all plots occurred between 26 and 30
April. The hatching period began on 15 May in all three plots and ceased
on 15 June in the moderately disturbed plot, on 5 June in the most dis-
turbed plot, and on 20 June in the least disturbed plot. The peak of hatch-
ing in all plots occurred between 20 and 24 May. Observations of the laying
and hatching periods in other parts of the colony suggested that the study
plots were synchronous with the entire colony.

Behavioral responses of the gulls—interplot comparisons.—To standard-
ize the data, the number of fights was divided by the number of gull pairs
represented by at least one adult on the territory during each experimental
disturbance and by minutes of observation, i.e., 30 min for pre- and post-
disturbance observation periods or by the duration of the disturbance ob-
servation period. The number of attacks on chicks and chick runs were
each divided by the number of chicks in the plot during each experimental

disturbance and by minutes of observation or by the duration of the disturbance.

Adult fights, chick runs, and attacks on chicks occurred rarely before disturbance, very frequently during disturbance, and commonly after disturbance in the moderately and most disturbed plots but only rarely in the least disturbed plot (Table 2). Gulls in all plots behaved similarly before disturbance began, exhibiting few of the monitored behaviors (Table 2; ANOVAs, $P > 0.05$). Behavior was similar in the moderately and most disturbed plots for the disturbance or post-disturbance observation periods (ANOVAs, $P > 0.05$). In contrast, almost all behaviors were significantly more frequent in these plots compared to the pre-disturbance and post-disturbance observation periods in the least disturbed plot (*t*-tests, $P < 0.05$). Pecking rate after disturbance in the moderately disturbed plot was not higher than in the least disturbed plot ($P < 0.10$).

Behavioral responses of the gulls—intraplot comparisons.—There were no significant differences in behavior between the pre- and post-disturbance observation periods in the least disturbed plot (Table 2). In the moderately disturbed plot, adult fighting, chick runs, and attacks on chicks were more frequent during disturbance than in the pre- and post-disturbance observation periods (*t*-tests, $P < 0.01$). Pecks per attack and chick running were more frequent after disturbance than before (*t*-tests, $P < 0.05$), whereas adult fights and adult attacks on chicks ($P < 0.10$) did not differ for pre- and post-disturbance observation periods in the moderately disturbed plot.

In the most disturbed plot, chick runs, attacks on chicks, and pecking rate were higher during and after disturbance than before human intrusion (*t*-tests, $P < 0.01$; Table 2). Adult fights were more frequent during disturbance than in the pre-disturbance observation period ($t = 5.06$, df = 8, $P < 0.01$), but not different between the pre- and post-disturbance observation periods. All behavior measures except pecking rate were greater during disturbance than after in the most disturbed plot (*t*-tests, $P < 0.01$). Pecking rate remained at comparable levels during and after investigator entry.

Behavioral responses of the gulls—temporal patterns.—Adults became more aggressive and chicks ran more often in the more frequently disturbed plots over the course of investigator visits whereas the behavior of least disturbed gulls remained relatively constant. There were no significant trends in any plot for pre-disturbance observation periods. In the moderately disturbed plot, fights, attacks on chicks, and chick runs became more frequent later in the experiment during disturbances (Spearman rank correlations, $P < 0.05$) whereas only adult fights increased

TABLE 2
STANDARDIZED BEHAVIOR MEASURES FOR PRE-, DURING AND POST-DISTURBANCE OBSERVATION PERIODS IN EACH PLOT IN 1977

Plot	Adult fights[a]			Chick runs[a]			Attacks on chicks[a]			Pecks/attack		
	pre-	during	post-	pre-	during	post-	pre-	during	post-	pre-	during	post-
Least disturbed	0.02[b] ±0.02	—	0.03 ±0.04	0.00 ±0.00	—	0.00 ±0.00	0.00 ±0.00	—	0.00 ±0.00	0.00 ±0.00	—	0.00 ±0.00
Moderately disturbed	0.03[c] ±0.04	3.49[c,d,e] ±2.60	0.35[c] ±0.29	0.00 ±0.00	4.45[c,d,e] ±3.23	0.25[c,d] ±0.30	0.01 ±0.02	6.31[c,d,e] ±5.75	0.51[c] ±0.74	0.33 ±1.00	1.98[c,d] ±0.81	1.93[d] ±1.53
Most disturbed	0.04 ±0.06	5.61[c,d,e] ±3.01	0.96[c] ±1.06	0.00 ±0.00	3.42[c,d,e] ±2.46	0.45[c,d] ±0.37	0.01 ±0.01	4.25[c,d,e] ±2.62	1.07[c,d] ±0.92	0.11 ±0.33	2.51[c,d] ±0.89	2.69[c,d] ±0.90

[a] Values shown were multiplied by 100.
[b] All values are mean ± 1 SD.
[c] Statistically different (t-tests, $P < 0.05$) from the same behavior before and after disturbance in the least disturbed plot.
[d] Statistically different (t-tests, $P < 0.05$) from the same behavior before disturbance in the same plot.
[e] Statistically different (t-tests, $P < 0.05$) from the same behavior after disturbance in the same plot.

TABLE 3
FATES OF CHICKS AND MEAN DATE OF OCCURRENCE FOR EACH FATE IN EACH STUDY
PLOT IN 1977

| Plot | Adopted | | Disappeared | Died on natal territory | Pecked to death |
	inside plot	outside plot			
Least disturbed	2 (0)[a]	0 (0)[a]	2 (0)[a]	6 (1)[a]	2 (0)[a,b]
	(21 May)		(25 May)	(30 May)	(8 June)
Moderately disturbed	7 (1)[a]	10 (0)[a]	12 (3)[a]	5 (1)[a]	16 (0)[a]
	(25 May)[d]		(25 May)[d]	(26 May)[c]	(30 May)[c,d]
Most disturbed	6 (0)[a]	22 (0)[a]	15 (0)[a]	7 (0)[a]	25 (0)[a]
	(23 May)[d]		(21 May)[d,e]	(26 May)[d]	(29 May)[d,e]

[a] The number in parentheses represents chick losses after experimental disturbances were stopped.
[b] These deaths were caused by adoption of chicks from the most disturbed plot (see text).
[c] *t*-test, $P < 0.05$.
[d] *t*-test, $P < 0.01$.
[e] *t*-test, $P < 0.001$.

throughout the experiment during the post-disturbance observation period ($r_s = 0.66$, df = 9, $P < 0.05$). In the most disturbed plot, adult fights, attacks on chicks, pecks per attack, and chick runs increased throughout the experiment during and after disturbances (Spearman rank correlations, $P < 0.05$).

Chick fates, 1977.—The number of chicks dying on territory was similar in all plots (Table 3). However, adoptions ($\chi^2 = 41.67$, df = 1, $P < 0.005$), chick disappearances ($\chi^2 = 18.61$, df = 1, $P < 0.005$), and pecking deaths ($\chi^2 = 33.38$, df = 1, $P < 0.005$) were more common in the most disturbed plot than in the least disturbed area. Similarly, these chick fates occurred more in the moderately disturbed plot than in the least disturbed plot (adoptions: $\chi^2 = 12.19$, df = 1, $P < 0.005$; disappearances: $\chi^2 = 6.98$, df = 1, $P < 0.01$; pecking deaths: $\chi^2 = 9.18$, df = 1, $P < 0.005$). Chicks in the most disturbed plot were adopted ($\chi^2 = 10.04$, df = 1, $P < 0.005$) and pecked to death ($\chi^2 = 8.06$, df = 1, $P < 0.005$) more frequently than those in the moderately disturbed plot.

To determine whether each chick fate occurred at different times during the experiment, I compared the dates on which adoptions, chick killings, chick deaths on territory, and disappearances occurred for each plot. There were no differences in date of occurrence for any of these chick fates in the least disturbed plot (Table 3). In the moderately disturbed plot, adoption and disappearance occurred nearest the onset of hatching, death on the territory ranked third, and chick killings occurred latest. Adoption ($t = 3.96$, df = 32, $P < 0.01$), disappearance ($t = 4.36$, df = 29, $P < 0.01$),

TABLE 4
REPRODUCTIVE PERFORMANCE FOR EACH QUARTER OF POST-HATCHING PERIOD IN EACH PLOT ON MUGG'S ISLAND IN 1977

Plot	Quarter of the season	Eggs laid	Eggs hatched (hatching success) %	Fledglings (fledging success) %	Net reproductive output %
Least disturbed	1	61	59 (97)	58 (98)	95
	2	63	62 (98)	62 (100)	98
	3	61	53 (87)	49 (93)	80
	4	60	53 (88)	46 (90)[a]	79[a]
	Total	245	227 (93)	215 (95)[a]	89[a]
Moderately disturbed	1	54	49 (91)	40 (82)	74
	2	56	52 (93)	43 (83)	77
	3	57	50 (88)	39 (78)	68
	4	57	50 (88)	33 (66)	58
	Total	224	201 (90)	154 (77)	69
Most disturbed	1	40	34 (85)	16 (47)	40
	2	39	37 (95)	28 (76)	72
	3	39	30 (77)	16 (53)	41
	4	39	23 (59)	11 (48)	28
	Total	157	124 (79)	71 (57)	45

[a] Percentages calculated after excluding two chicks pecked to death by their own parents (see text).

and death on the territory ($t = 2.32$, df = 20, $P < 0.05$) were significantly earlier events than chick killings.

The pattern was very similar in the most disturbed plot, where adoptions occurred earlier than pecking deaths ($t = 2.88$, df = 51, $P < 0.01$) and disappearances were earlier than pecking deaths ($t = 8.73$, df = 38, $P < 0.001$) and deaths on territory ($t = 3.00$, df = 20, $P < 0.01$). Thus, chick fates tended to occur in the following temporal sequence: disappearance, adoption, deaths on territory, and chick killing.

Reproductive Performance, 1977

Hatching success in the most disturbed plot was lower than in the least and moderately disturbed plots ($\chi^2 = 16.32$, df = 2, $P < 0.005$; Table 4). Birds in the most disturbed plot had the lowest fledging success, those in the least disturbed plot had the highest, and those in the moderately disturbed area had intermediate success ($\chi^2 = 71.32$, df = 2, $P < 0.005$; Table 4). Net reproductive output followed the same pattern ($\chi^2 = 83.43$, df = 2, $P < 0.005$).

Late nesters in the least disturbed plot had poorer reproductive perfor-

TABLE 5

REPRODUCTIVE PERFORMANCE OF RING-BILLED GULLS IN INVESTIGATIONS DURING WHICH
STUDY PLOTS WERE ENTERED FREQUENTLY THROUGHOUT NESTING SEASON

Study site or lake	Year	Total nests	Hatching success Mean (%)	Fledging success Mean (%)	Fledglings per nest Mean	Fledglings per egg laid Mean (%)	Source
Mackinac Str.,	1952	16	—	31	67	22	Emlen (1956)
Michigan	1953	20	72	—	—	—	
Miquelon L.,	1964	87	86	34	1.00	29	Vermeer (1970)
Alberta	1965[a]	436	16	00	00	00	
L. Huron	1972	80	63	87	1.54	55	Dexheimer and
	1972	107	60	70	1.19	42	Southern (1974)
Gull Is.,	1976	193	86	—	—	—	Chardine (1978)
L. Ontario	1977	155	78	81	1.84	63	
Granite Is.,	1976	144	89	58	1.53	52	Somppi (1978)
L. Superior	1977	405	62	67	1.04	33	
E. Headland,	1977	183	81	40[b]	1.35[b]	33[b]	Haymes and
L. Ontario							Blokpoel (1978)
Mugg's Is.,	1976	166	82	79	1.76	65	this study
L. Ontario	1977[c]	75	90	77	2.05	69	
	1977[d]	53	79	58	1.34	45	
Mean	—	—	77	62	1.40	46	
Min-max	—	—	60–90	31–87	0.67–2.05	22–69	
SD	—	—	11	20	0.41	16	
N	—	—	12	11	11	11	

[a] Data excluded from total and mean.
[b] N = 93.
[c] Moderately disturbed plot.
[d] Most disturbed plot.

mance than early or mid-season nesters (hatching success: $\chi^2 = 9.18$, df = 3, $P < 0.005$; fledging success: $\chi^2 = 8.31$, df = 3, $P < 0.01$; net reproductive output: $\chi^2 = 17.42$, df = 3, $P < 0.005$; Table 4). There were no seasonal differences for reproductive performance in the moderately disturbed plot even though late nesters tended to have lower success. In the most disturbed plot, hatching success was lower for late nesters ($\chi^2 = 16.30$, df = 3, $P < 0.005$) whereas net reproductive output was lower for early and late breeders ($\chi^2 = 16.36$, df = 3, $P < 0.005$). Fledging success followed a pattern similar to net reproductive output ($P < 0.10$).

Reproductive Performance in Other Years

Hereafter, I use the term 'traditional disturbance' when referring to studies in which investigators (including myself) entered study areas at

TABLE 6

REPRODUCTIVE PERFORMANCE OF RING-BILLED GULLS IN THIS INVESTIGATION WHEN
VISITS TO STUDY PLOTS WERE RARE OR ABSENT DURING POST-HATCHING

Study-site	Year	Total nests	Hatching success	Fledging success (%)	Fledglings/ nest (%)	Fledglings/ egg laid	Source
Mugg's Is.	1977[a]	85	93	95	2.53	89	this study
Mugg's Is.	1978	40	83	91	2.14	73	this study
E. Headland	1980	172	—	—	2.34[b]	—	this study
Mean	—	—	87	94	2.37	81	
Min-max	—	—	83–93	91–95	2.14–2.53	73–89	
SD	—	—	9	2	0.20	11	
N	—	—	2	2	3	2	

[a] Least disturbed plot.
[b] Revised estimate included in overall mean (see text).

least every second day throughout the breeding season. I distinguish these studies from some of the research reported here by using the term 'minimal disturbance' to refer to circumstances where I reduced or eliminated investigator disturbance during the post-hatching period.

Mugg's Island 1976–1978 and Eastern Headland 1980.—Using minimal disturbance techniques on Mugg's Island (1977—least disturbed plot, 1978—plot three) and on the Eastern Headland, reproductive performance was consistently better than when I followed traditional methods (Mugg's Island, 1976—plots one, two, and three; 1977—moderately and most disturbed plots; Tables 5 and 6). After minimizing disturbance, hatching success averaged 8% higher, fledging success averaged 19% higher, fledglings per nest averaged 36% higher, and net reproductive output averaged 26% higher.

When the gulls were not disturbed during post-hatching on Mugg's Island in 1978, late nesters had lower fledging success than early or mid-season nesters ($\chi^2 = 10.59$, df = 3, $P < 0.05$), but hatching success and net reproductive output did not vary significantly with time of hatching ($P < 0.10$; Table 7).

Reproductive Performance in Other Studies

Reproductive performance for Ring-billed Gulls investigated under traditional disturbance conditions in this and other studies varied considerably (Table 5) but was consistently higher under minimal disturbance conditions than under traditional disturbance conditions (fledging success 52% higher, Mann-Whitney U-test, $P < 0.05$; fledglings per nest 71% higher,

TABLE 7
REPRODUCTIVE PERFORMANCE FOR EACH QUARTER OF POST-HATCHING PERIOD IN 1978

Quarter of the season	Eggs laid	Eggs hatched (hatching success) %	Fledglings (fledging success) %	Net reproductive output %
1	28	25 (89)	23 (92)	82
2	29	26 (90)	25 (96)	86
3	32	24 (75)	24 (100)	75
4	31	24 (77)	18 (75)	58

Mann-Whitney U-test, $P < 0.05$; and net reproductive output 76% higher, Mann-Whitney U-test, $P < 0.05$; Tables 5, 6). Only hatching success was not significantly higher when disturbance was minimized.

DISCUSSION

Observation of Investigator Activity and Gull Behavior, 1977

Confounding factors.—Interplot differences in nesting chronology, age composition, gull density or vegetation may have affected the results. Nesting chronologies for each plot were similar, so any behavioral differences due to different temporal patterns of egg-laying and/or hatching should have been consistent across plots. Judging by the proportion of pairs with one member having immature plumage (black pigment in rectrices, brown primaries without white spots, brown feathers on breast, belly, or head), each plot had a similar age composition (least disturbed plot [17%], moderately disturbed plot [12%], most disturbed plot [13%]). Nesting density was highest in the least disturbed plot (0.7 nests/m²), intermediate in the moderately disturbed plot (0.6 nests/m²) and lowest in the most disturbed plot (0.5 nests/m²). The high fledging success in the least disturbed plot demonstrates that density-dependent chick mortality was not an important factor when human activity was curtailed.

Sparse willows grew near the edges of the least and moderately disturbed plots and were absent in the most disturbed area, but the vegetation provided very little cover. When chicks ran from their natal territories, they infrequently used willows for cover so confounding effects were probably minimal. Proportionately more pairs in the most disturbed (75%) and moderately disturbed (65%) plots nested in the driftwood half of the plot than in the least disturbed plot (52%). Driftwood provided more hiding places for chicks during disturbance than open areas so relatively more young in the more disturbed plots could have benefitted from driftwood.

Generally then, confounding factors were of minor importance compared to the effects of investigator activity.

Behavioral responses of the gulls.—Human activity grossly altered adult and chick behavior. Adults fought 10–15 times more often during disturbance than before and attacks on chicks increased between 400 and 600 fold. I never observed a chick run during pre-disturbance watches and yet runs were very common during and after disturbance. Chick running and adult attacks persisted at high levels after investigator activity. As a result, most pecking deaths occurred after disturbance because adult fighting subsided compared to disturbance observations and running chicks became easier targets for attack.

Chick running during investigator visits has been reported in many Laridae (Herring Gull: Paynter 1949, Tinbergen 1960; Glaucous-winged Gull: Vermeer 1963, Gillett et al. 1975; Western Gull: Robert and Ralph 1975; Ring-billed Gull: Emlen 1956; California Gull [*L. californicus*]: Vermeer 1970; Heermann's Gull [*L. heermanni*]: Anderson and Keith 1980; Sooty Tern [*Sterna fuscata*]: Ashmole 1963). I have observed chick running in response to my presence in Herring Gull, Caspian Tern (*S. caspia*), and Common Tern (*S. hirundo*) colonies. Thus, chick running resulting from human activity may be the rule among terrestrial-nesting larids.

In this study, chick running caused by investigator activity combined with seasonal differences in adult behavior and resulted in different chick fates. Early in the post-hatching period running chicks were either adopted by incubating or brooding adults or they ran long distances (usually >5 m) from their territories and disappeared. Chicks that were not adopted probably starved to death or died of exposure elsewhere in the colony. Later in the post-hatching period, chicks ran more often and increasingly hostile neighbors frequently killed chicks of fewer than 10 days of age. These seasonal differences in chick mortality contributed to different reproductive performance for early, mid-season, and late nesters in the most disturbed plot. Adult aggression increases in other terrestrial nesting larids as chicks become more mobile (Western Gull: Hunt and Hunt 1975; Herring Gull: Burger 1980, Fetterolf, unpubl.; Ring-billed Gull: Fetterolf 1981). As in this study, disturbance in previous investigations may have amplified adult aggression leading to artificially higher rates of pecking death for late hatching chicks.

In contrast to disturbed situations, increases in adult aggressiveness during the post-hatching period (Fetterolf 1981) resulted in very few chick deaths from neighbor attack in undisturbed conditions (Fetterolf, in press). During 1976–1978, I observed undisturbed Ring-billed Gulls for more than 450 h and saw only three pecking deaths while watching more than 1100 chicks being reared (Fetterolf, in press). I saw no pecking deaths in more

than 200 h of observation on 55 pairs of minimally disturbed Herring Gulls in 2 years. In both these species, brood reductions of other kinds were also uncommon when human activity was rare or eliminated after hatching began. Young in artificially smaller broods resulting from investigator disturbance probably had less intra-brood competition for provisions than chicks in minimally disturbed broods and thus attained better physical condition (e.g., greater fat stores) at fledging.

Other potentially important biases resulted from a high frequency of adoption which is rare under minimal disturbance conditions. On two occasions, adoptive parents with eggs pecked their newly hatched chicks to death. Parents with young chicks often adopted chicks larger (older) than their own. Victims of this artificially skewed competition usually appeared thin and weak and occasionally seemed to starve to death. Measures of chick quality such as growth rate, weight at fledging, fat load, etc., could be seriously biased by unnatural brood reductions and adoptions, thus creating severe interpretational problems (in parental investment research for example, Trivers 1972).

Reproductive Performance, 1977

Hatching success was lowest in the most disturbed plot where nest checks were shortest before the post-hatching period. Longer disturbances and direct entry to the plot during experimental disturbances in post-hatching therefore reduced hatching success compared to the moderately and least disturbed plots. Entering the plot increased adult fighting which forced incubators off nests more frequently for longer periods and probably increased embryonic mortality due to excessive cooling or heating.

Fledging success, and consequently net reproductive output, were seriously affected by human activity. Even when investigator activity was restricted, the loss of young birds was significant. First, investigator activity in this study was limited to every second day until nearly all eggs were hatched and stopped once the youngest chicks were 7 days old. In contrast, post-hatching reproductive performance is usually assessed by entering study areas at least every second day until all chicks reach a minimum of 21–37 days of age (Vermeer 1970, Dexheimer and Southern 1974, Chardine 1978, Haymes and Blokpoel 1978, this study 1976). Second, human activity was also restricted in the moderately disturbed plot by limiting the duration of visits and by walking the perimeter of the plot. Nevertheless, chick losses were high.

Reproductive Performance in Other Years and Other Studies

Hatching success on Mugg's Island in 1976 and 1978 was comparable and intermediate between the most disturbed plot and moderately dis-

turbed plots in 1977. Interyear differences in age composition (pairs in adult plumage, 1976—39%, 1978—100%) and nocturnal predation (nightly visits by a Great Horned Owl [*Bubo virginianus*] in 1978) confound interpretations regarding the impact of human disturbance. No doubt such differences exist among investigations as well, so low hatching success often reported in other studies could be attributable to more frequent or prolonged human disturbance or to other factors.

Generally, fledging success, fledglings/nest, and net reproductive output on Mugg's Island in 1976 and 1977 (moderately and most disturbed plots) fell within the range of values reported in past research but were demonstrably lower than in less disturbed situations. In a similar 2-year study of human disturbance in Herring Gulls, I found fledging success of 81–100%, and net reproductive output of 81–91% in plots that were rarely entered during the post-hatching period (Fetterolf 1979b). By comparison, in plots that were disturbed regularly throughout post-hatching, fledging success was 46–50% and net reproductive output was 24–37%. Caspian Terns also have remarkably high fledging success (90–98%) and net reproductive output (78–79%) when they are not disturbed by investigators during the post-hatching period (Fetterolf and Blokpoel, in press). Infrequently disturbed Glaucous-winged Gulls had about 89% fledging success compared to 73% for birds that were more frequently disturbed (Gillett et al. 1975). Young of the cliff-nesting Black-legged Kittiwake (*Rissa tridactyla*) do not run (Cullen 1957) and fledging success of kittiwakes approaches 90% even for pairs nesting for the first time (Wooler and Coulson 1977).

The high fledging success in minimally disturbed studies is exceptional compared to traditional studies of terrestrial-nesting Laridae (e.g., Paynter 1949, Vermeer 1963, Harris 1964, Kadlec and Drury 1968, Kadlec et al. 1969, Hunt and Hunt 1976; see Table 5). Reduced reproductive performance resulting from human activity has been reported by Hunt (1972), Robert and Ralph (1975), Gillett et al. (1975), Hand (1980), and Anderson and Keith (1980). Although frequent disturbances by a mammalian predator such as a fox (*Vulpes* sp.) might induce similar mortality in larids, the combination of human disturbance, increasing adult aggression, and increasing chick mobility may have caused artificial chick losses in previous studies which cannot be separated from real biological effects.

Seasonal patterns as well as the amount of chick mortality may be affected by human disturbance. When nesters were rarely disturbed in 1977 or not disturbed in 1978 during post-hatching, late nesters had lower reproductive performance. A similar seasonal pattern of reproductive performance has been found in other investigations on gulls (see Parsons 1975, Morris and Haymes 1977 for reviews). Evidence presented here sug-

gests that this pattern in previous studies may have been enhanced but not modified by human disturbance. Also in support of this interpretation, Robert and Ralph's (1975) results show that late hatching eggs in frequently disturbed plots had lower hatching success and higher losses of young chicks than late hatching eggs in less frequently disturbed areas. Patterson (1965) reported that early and late Black-headed Gulls (*L. ridibundus*) had lower reproductive performance and Parsons (1971) attributed higher early and late season chick mortality in Herring Gulls to cannibalism. High mortality for early and late nesters occurred in the most disturbed plot in 1977 but was not apparent under minimal disturbance conditions, so this pattern may have been created by human disturbance in some previous investigations.

Theoretical considerations.—Since the development of sound theory regarding the evolution of reproductive strategies in colonial birds depends upon real unbiased biological patterns of mortality, human activity has potentially caused numerous biases. Has investigator activity changed the probability of survival to reproductive age of individual chicks (effective survivorship)? The question is important because if effective survivorship is not changed by human disturbance, human activities would have no negative impact on population dynamics or on biological theory. My data provide no direct answer to the question but suggest that effective survivorship is changed by human disturbance. For example, chick death could have been random instead of the result of selection acting against inferior (in the absence of disturbance) individuals. Second, chick death could have been non-random resulting from selection against individuals that behaved in a more 'life-threatening' manner during human disturbance. Finally, artificial brood reductions may enhance effective survivorship of individuals remaining with their parents whereas increases in brood-size due to adoption may have the opposite effect. I believe these findings, in concert with those of previous investigators (e.g., Gillett et al. 1975, Robert and Ralph 1975) compel future researchers of terrestrial-nesting larids to ask: how successful are the birds when they are undisturbed by humans during the post-hatching period (see Duffy 1979)?

SUMMARY

I documented the effects of human disturbance on gull (*Larus* sp.) behavior and reproductive performance in two different colonies between 1976 and 1980 by observing gull behavior and reproductive performance during periods with different levels of investigator activity. Human disturbance precipitated changes in gull behavior which caused significant reductions in fledging success, fledglings per nest, and net reproductive output even when disturbance was limited. In contrast, areas which were relatively undisturbed during the post-hatching period in 3 years and two colonies had very few chick deaths. Human disturbance caused adoptions and enhanced seasonal patterns of chick mortality. I conclude that

human-induced chick losses could have had confounding effects in most past studies in-
volving larid reproductive success and may seriously confound theoretical interpretations of
reproductive strategies in terrestrial-nesting colonial birds.

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DEPT. ZOOLOGY, UNIV. TORONTO, TORONTO, ONTARIO M5S 1A1, CANADA.